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Cumulative herbivory outpaces compensation for early floral damage on a monocarpic perennial thistle

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Abstract

Floral herbivory represents a major threat to plant reproductive success, driving the importance of plant tolerance mechanisms that minimize fitness costs. However, the cumulative insect herbivory plants experience under natural conditions complicates predictions about tolerance contributions to net fitness. Apical damage can lead to compensatory seed production from late season flowering that ameliorates early season fitness losses. Yet, the compensation realized depends on successful development and herbivore escape by later season flowers. Using monocarpic perennial *Cirsium canescens*, we quantified seed-reproductive fitness of plants with vs. without experimental damage to the early-developing large apical flower head, with and without a 30–40% herbivory reduction on subsequent flower heads, for two flowering cohorts. Plants with reduced herbivory clearly demonstrated the release of apical dominance and compensation, not overcompensation, for apical damage via greater seed maturation by later flower heads. In contrast, plants that experienced ambient herbivory levels on subsequent heads undercompensated for early apical damage. Individuals had lower total seed set when the apical head was damaged. Compensation was, therefore, possible through a small increase in total flower heads, caused by a higher rate of floral bud survival, and a higher seed maturation rate by subsequent heads, leading to more viable seeds per matured flower head. With ambient cumulative floral herbivory, compensation for apical damage was not sufficient to improve fitness. Variation in the intensity of biological interactions played a role in the success of plant tolerance as a mechanism to maximize individual fitness.

Keywords Apical dominance · Floral herbivory · Plant–herbivore interactions · Plant tolerance · Predispersal seed predation

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Introduction

Insect destruction of developing inflorescences and seeds, i.e., floral herbivory or predispersal seed predation, represents a challenge to plant fitness. Such herbivory can dramatically and quantitatively reduce plant-reproductive success (Louda and Potvin 1995; McCall and Irwin 2006; Lucas-Barbosa 2016) and directly affect plant population growth rate (Rose et al. 2005; Tenhumberg et al. 2008; von Euler et al. 2014) and population density (Louda 1983; Jongejans et al. 2008; Lehdal et al. 2016). Floral herbivore impacts should, therefore, favor plant growth and allocation strategies that can reduce losses, or even improve fitness, under herbivory pressure (Fornoni 2011; Agrawal et al. 2012; Carmona and Fornoni 2013). However, these strategies likely require allocation tradeoffs that can additionally influence fitness outcomes. Consequently, it can be difficult to evaluate emergent fitness benefits from plant responses under natural

conditions (Agrawal 2005; Brody et al. 2007; Klimešová et al. 2007).

Tolerance strategies, such as growth or resource allocation that compensate for herbivore damage, offer one possibility to mitigate fitness costs from herbivory (tolerance: Strauss and Agrawal 1999; Stowe et al. 2000), albeit at additional cost. For instance, compensatory allocation to subsequent or additional flowers can minimize the influence of herbivore floral damage on plant fitness (e.g., Pilsen and Decker 2002; Brody et al. 2007; Wise et al. 2008), and even increase within-year fitness relative to undamaged plants (overcompensation, e.g., Paige 1992; Lennartsson et al. 1998; Agrawal 2000). However, resulting phenological delays or under-allocated resource reserves may limit fitness gains, particularly if a tolerance response is not triggered (Lehtilä 2000; Järemo and Palmqvist 2001; Klimešová et al. 2014). Tolerance can, therefore, present an ecological bet-hedging tradeoff: the risk of complete fitness loss (fitness variance) minimized at the expense of maximizing mean individual fitness (i.e., Childs et al. 2010; Starrfelt and Kokko 2012). Plant damage responses may thus lead to variable individual results. Whether such outcomes further translate to significant directional population-level impacts is often unknown (Lay et al. 2011; Low et al. 2013; Aikens and Roach 2015). More research on plant responses under natural field conditions is needed to provide information on key aspects of tolerance, such as the relative fitness contributions of response strategies versus the fitness impacts of cumulative herbivory, and how variation in the growth and herbivory environment drives emergent tolerance benefits.

We experimentally evaluated the fitness contribution of strong early-season apical investment (prioritized investment in early season apical seed production) and compensatory reproductive effort in response to apical damage (high investment in seed production from multiple later flowers) under conditions of low and high floral attack in *Cirsium canescens* Nutt. (Platte thistle). This monocarpic perennial species is known to have strong population-level interactions with floral herbivores (Louda and Potvin 1995; Rose et al. 2005; Russell and Louda 2005; Rand and Louda 2012), and would be expected to benefit from tolerance strategies. Apical meristem damage is generally a common occurrence imposed by physical or biological factors (Gruntman and Novoplansky 2011; Adhikari and Russell 2014; Klimešová et al. 2014) and represents a disproportionately large potential early-season fitness risk for *C. canescens*. When the apical flower head escapes damage, it contributes substantially to plant fitness ($\pm 50\%$ total seed production, Louda and Potvin 1995). However, up to 50% of flowering *C. canescens* per season may have the apical flower head aborted by early insect feeding (Lamp 1980). Compensatory responses for within-season herbivory should supply important fitness

benefits for this monocarpic plant, providing a relevant system in which to examine tolerance in the field.

We asked three questions: (1) Does apical damage lead to a detectable tolerance response (i.e., change in within-plant distribution of flowering effort and seed production relative to undamaged plants)?; (2) Do apical damage responses interact with cumulative insect floral herbivory pressure in determining total seed reproduction by *C. canescens*?; and, (3) Does variation in the risk of cumulative floral herbivory on the later-flowering heads affect realized plant fitness outcomes, and therefore, fitness gains, from the plant tolerance response? We expected compensation for apical flower damage to result from an increase in branches or matured flowers, due to release from apical dominance restraints. Such compensation could additionally change plant phenology, aiding flower escape from herbivores in time (Aarssen 1995; Lehtilä 2000; Gruntman and Novoplansky 2011). Apical damage has led to compensation, and occasionally overcompensation, for herbivore damage in other systems. Haphazard variation in the timing and duration of insect herbivory and flowering delays due to apical damage can, however, reduce the likelihood of successful seed production and limit the reliability of fitness gains from compensation (Huhta et al. 2000; Brody and Irwin 2012; Adhikari and Russell 2014). This variability increases the potential value of strong early-season apical investment, relative to fitness costs spread across multiple later flowering heads, when fitness must be realized under cumulative season-long insect pressure. Thus, outcomes from resultant tradeoffs are uncertain when valuable early-season apical investments affect the timing and quantity of later flowers. The experimental results clearly demonstrate compensatory ability, but ecological constraints on the benefits of the compensatory tolerance response.

Materials and methods

Study system

Cirsium canescens Nutt. (Platte thistle) is a short-lived, monocarpic perennial that is native to sand and gravel soils of the upper Great Plains and southern Rocky Mountains (Kaul et al. 2007). Prior research documented intense insect floral herbivory on *C. canescens*, including on the apical flower head (Lamp and McCarty 1981; Louda et al. 1990), that was variable among individuals (Louda and Potvin 1995). Seed loss significantly reduced average individual fitness and population density (Louda and Potvin 1995), and significantly lowered population growth rate (Rose et al. 2005), suggesting the possibility of strong selection pressure for compensatory response by this taprooted monocarpic plant.

Cirsium canescens grows as a rosette for 2–8 years prior to its reproductive year (Louda and Potvin 1995), and flowers from mid to late May through late June. Reproduction is solely by seed and flowering is determinate, beginning with the terminal apical flower head (Lamp 1980; Kaul et al. 2007). Over the season, subsequent flower heads develop basipetally, flowering sequentially from the terminal apical head down the stem and sequentially within each branch below the branch terminal head.

The five main native floral and seed-feeding herbivores at our site were: two tephritid flies (*Paracantha culta* Wiedemann, *Orellia occidentale* Snow), two pyralid moths [*Pyrausta subsequalis* Gn., *Homoeosoma eremophasma* Neunzig (complex)], and a weevil (*Baris* nr. *subsimilis* Walker) (Lamp 1980; Louda and Potvin 1995). In addition, the Eurasian flower head weevil (*Rhinocyllus conicus* Frölich) invaded the floral-feeding guild in 1993 (Louda et al. 1997; Louda 1998). Previous studies document both the feeding damage (Lamp and McCarty 1981) and the population-level impacts (Louda et al. 1990; Louda and Potvin 1995; Rose et al. 2005; Russell and Louda 2005) by these six floral herbivores.

Study sites

The study extended across six interconnected sand prairie sites in Arthur County, western Nebraska, in the upper Great Plains, USA. Three sites were within Arapaho Prairie Preserve, a 1200 ha reserve owned by The Nature Conservancy and managed for research by the University of Nebraska Cedar Point Biological Station (Keeler et al. 1980). Three additional sites were in private pasturelands surrounding Arapaho Prairie; these are managed for sustained long-term cattle production (Delwin Wilson, personal communication).

Experimental design

We used a 2×2 factorial completely randomized design, to evaluate the effect of apical head damage and cumulative floral herbivory over the season on adult plant herbivory tolerance. We conducted the experiment twice (2007, 2008) using the same design for each year's flowering cohort. We manipulated apical head damage (A) to compare plants with apical head damage deliberately imposed (A_D) versus with no damage imposed (A_N). Within each apical damage treatment, we altered cumulative floral herbivory (H) on subsequent, lower-positioned flower heads to compare plants with reduced herbivory (H_R : insecticide-in-water) versus with ambient herbivory (H_A : water-only control). Thus, we had four treatment groups: (1) experimentally damaged apical head with reduced cumulative herbivory on lower (later) heads ($A_D \times H_R$); (2) experimentally damaged apical head damage with ambient levels of cumulative herbivory on

lower heads ($A_D \times H_A$); (3) undamaged apical head with reduced cumulative herbivory on lower heads ($A_N \times H_R$); and, (4) undamaged apical head with ambient cumulative herbivory on lower heads ($A_N \times H_A$).

In early season each year, we selected and marked plants that were likely to mature and flower, evidenced by an apical flower head bud within the center of the rosette (5–10 May 2007, 26 April–10 May 2008). New plants had to be chosen each year. In 2007, we had 15 replicates of the 4 treatments (total $n = 60$ plants). In 2008, we increased the number of replicates to 35 (total $n = 140$ plants). Each replicate block consisted of four plants matched by initial plant and apical flower head sizes to control for any effect of variation in early-season size or phenology on treatment response. Initial size was measured as a combination of rosette diameter (cm), apical bud diameter (mm), and total number of flower head buds already initiated. We assigned the four treatment combinations randomly within each replicate block.

We imposed damage on the apical flower head of the two plants randomly assigned to the damage treatment within each replicate (A_D). Our damage treatment was designed to emulate the flower bud damage and insect feeding we observed in the field, which severely slows or stops apical flower head development. To impose damage in 2007, we caged three field-collected thistle insects onto the flower head in 1 mm mesh bags for 1 week in early season (one early instar native moth larva, *P. subsequalis*, plus two small adult native weevils, *B. subsimilis*) after drilling a small hole (< 1 mm diameter) into the lower part of each flower head to facilitate moth larva entry. After a week, if the damage imposed was not comparable to that observed to impede flower head development naturally, we further damaged the head using a razor blade to partially sever vascular transport from one side of the stem into the flower head, similar to insect mining damage. In 2008, early insect abundances were low. Thus, we set up five replicates using insects as in 2007, and an additional 30 replicates using only mechanical damage (drilled hole + partial girdling). The effects of the two apical damage techniques (insect + mechanical damage vs. mechanical damage only) did not differ in their effect on seed production; thus, we present the combined data. Apical heads assigned to the undamaged treatment (A_N) were handled but not damaged, and also were treated with insecticide to prevent later apical damage.

We manipulated insect floral herbivory among individuals during the season, reducing cumulative floral herbivory (H_R , insecticide-treated later heads) or allowing ambient herbivory for a control (H_A , water-treated heads) on one plant in each of the apical damage treatments per replicate. In the insecticide treatment, we reduced cumulative floral herbivory by individually spraying each non-apical flower head with insecticide-in-water before and after florets were

presented for pollination to avoid interfering with pollinators. In 2007, we used the insecticide Acephate (Isotox^R, Chevron Corp), applied every 7–10 days in a 1% solution, as recommended. In 2008, in an effort to increase insecticide effectiveness, we used the pyrethroid insecticide bifenthrin (FMC Corporation Pty Ltd.), applied every 14 days in a 0.06% solution.

Data collection

We measured initial plant and flower head sizes when replicate blocks were created and the treatments imposed (8–10 May 2007; 11–13 May 2008). We then measured the magnitude and the distribution of individual plant-reproductive effort every 2 weeks in 2007 (to 31 July), and every 4 weeks in 2008 (1–3 June, 1–3 July, 29 July–2 Aug). On each sampling date for each plant, we recorded diameter (mm) of the terminal flower heads on all branches and counted the total number of smaller, subtending flower buds initiated on each branch. We also recorded: plant height (cm), rosette diameter (average of two perpendicular diameters, cm), total number of branches per plant (> 1 cm long), and total number of flower heads initiated per plant.

Fitness

To document plant seed production, we collected each flower head that matured (exserted at least one floret) for dissection as the flower heads and branches senesced. For each mature flower head collected, we recorded: mass (g), diameter (mm), number of developed undamaged seeds, and amount of internal insect damage (i.e., to inflorescence receptacle, florets, and developing seeds).

Insect damage

To quantify internal damage by insects, we divided each flower head into four sections and assigned a damage score to each quarter; this damage score was based on the percent area of the receptacle, florets, and seeds that were damaged: 0 = 0–1%; 1 = 1.1–10%; 2 = 10.1–50%; 3 = 30.1–50%; 4 = 50.1–75%; and 5 = 75.1–100%. The total damage score for each flower head was calculated as the average of the four individual quarter scores. For analysis, this total damage score was converted to the proportion represented by the midpoint of its damage interval (e.g., score 1 = 0.05, score 2 = 0.15, etc.), providing a conservative estimate of mean insect damage per flower head, as one relatively large interval (damage 5) represents the very high levels of damage (> 75%), compared to several smaller intervals that represent lower levels of damage.

Data analyses

Between experiment comparison and initial conditions

To evaluate whether initial size or between-year differences affected treatment outcomes, we analyzed initial size measurements (5–10 May 2007, 26 April–10 May 2008) for number of flower heads per plant, mean rosette diameter, and apical head diameter, as a composite-dependent variable representing plant size using MANOVA with Pillai's trace test statistic. We also analyzed both initial and final plant size estimates for between-year differences with MANOVA (Pillai's trace test statistic), followed by separate univariate ANOVAs for each separate measurement if the MANOVA results were significant. No significant differences in initial size occurred among the four treatments within year (treatment \times year: $p > 0.10$ for all variables). Plants were on average larger in 2007 than in 2008 (both initial and final size estimates: Appendix S2). We further analyzed the interaction between treatment and year in a similar manner, and found no significant qualitative differences in treatment effects between years on plant performance ($p > 0.10$ for all treatment \times year interactions). We also evaluated whether treatment effect on plant seed number differed significantly between years (mixed model with year as both a random and fixed effect, and branch as a covariate for plant size). There was no significant year effect ($p = 0.69$). We, therefore, combined the data from both years and incorporated year as either a random effect or covariate when appropriate. Analyses were performed in R (R Core Development Team 2016).

Insect damage

To determine the effectiveness of the insecticide treatment, we examined the amount of insect damage to later flowering heads using the arcsine-transformed mean proportion internal damage per flower head. Transformed proportions were evaluated in a mixed effects model, with year and plant as random effects.

Treatment effects

We followed a similar analytical framework to parse treatment effects on fitness outcomes in response to each of the three questions posed. We first tested for significance of the main effects and treatment interaction. Because floral herbivory is known to have strong fitness consequences in this system (i.e., Louda and Potvin 1995), and because herbivory had a significant main effect in nearly all analyses, when significant treatment interactions occurred in the global model, we examined the effect of apical damage (A_D versus A_N) within each herbivory treatment (H_A or H_R) to best

evaluate compensation for apical head loss as well as the overall effect of herbivory on the outcome of apical damage.

Potential versus realized seed production

To examine how any compensatory response led to absolute differences in potential seed production per plant among treatments, we calculated the expected (potential) seed production based on the number and size of heads initiated and the expected number of seeds per head. We used published regressions for the number of undamaged filled seeds expected in relation to flower head size to estimate seed production potential per head (Louda and Potvin 1995), and summed the per head values to estimate potential seed production per plant. To quantify the percent of the potential seed production that was actually realized per flower head in the field, we divided observed seed count per head by the expected seed production. This parameter allowed us to assess whether a plant displayed tolerance after apical damage by compensatory production of seed, under either reduced or ambient herbivory.

Question 1: Plant response to apical damage

Because any compensation response would likely incorporate multiple plant characters, we grouped measurements associated with two different aspects of the potential plant response into two multivariate response variables: (1) plant structural investment (plant height, rosette diameter, number of branches, and number of flower buds); and, (2) plant reproductive effort (number of buds that produced flowers, number of heads that matured and developed viable seed). We combined two measures of reproductive effort because many heads that matured (exerted at least one flower) were so heavily damaged that they did not succeed in producing any viable seeds (see Results below). We analyzed treatment effects on each of these two composite variables using MANOVA with year as an additive main effect to account for annual differences in plant size. When significant treatment effects or interactions occurred in a MANOVA, we examined treatment effects on each of the significant dependent variables using separate ANOVA contrasts. When ANOVAs were significant, we examined the effect of apical damage (A_D versus A_N) within each herbivory treatment (H_A or H_R).

Question 2: Compensation and apical damage—effects on whole plant seed production

With the high average levels of ambient floral herbivory in this system, many later flower heads produced only a few or zero undamaged seeds, resulting in a strongly zero-biased distribution. Therefore, we used maximum likelihood to determine the most appropriate distribution for analysis of

the pattern of plant seed production using a generalized linear model. The best fit was a negative binomial distribution (function `glm.nb`). When an interaction was significant in the overall linear model, we evaluated the effect of apical damage within insecticide treatment using separate models. We included year in the analysis as a covariate.

The total potential seed production and the actual, realized seed production (undamaged viable seeds) as a proportion of the potential total per plant were analyzed with generalized linear models, with significant interactions followed by separate evaluation of apical damage effects within herbivory treatment.

Question 3: Contribution of lower-positioned heads and floral herbivory to outcomes

To examine treatment effects on distribution of seed production within plants, we analyzed seed set per flower head by head position on a plant and by treatment, with plant and year as random variables, in a linear mixed effects model (`lme` function). The number of undamaged, filled (“good”) seeds per head was square root-transformed prior to analysis to meet ANOVA assumptions. Potential and realized seed production per flower head by treatment and by flower head position were analyzed with linear mixed effects models with plant as a random effect. Proportions were square root-transformed before analysis.

To allow full evaluation of the numerous analyses performed, we present summarized results in Table 2, with full statistical tables provided in the online Supporting Information (Appendices S3 and S4).

Results

Imposition of treatments and initial plant size

Visually, plants in the apical damage treatment appeared to differ in the severity of apical damage realized. However, apparent variation in severity did not drive differences in response between plants with more versus less severe apical damage (see Appendix S1 in Supporting Information). Average insect damage per non-apical head did not differ significantly between apical damage treatments within each herbivory treatment ($p_A = 0.64$, $t = 0.46$; Table 1A; Appendix 3A). However, the insecticide treatment did decrease damage 24.5–30.4% within each apical head treatment ($p_H < 0.01$, $t = 5.86$, Table 1A); from 72.9 and 78.5% with and without experimental apical damage with ambient herbivory to 48.4 and 48.1% with and without experimental apical damage with insecticide-reduced herbivory. Individual plants varied widely in the amount of cumulative damage to flower heads that they experienced, especially within

Table 1 End-of-season plant performance for *C. canescens* by treatment ($X \pm SE$) over 2 years: experimentally reduced subsequent floral herbivory (H_R) vs. ambient subsequent floral herbivory (H_A) on plants without (A_N) versus with (A_D) experimental apical damage

	Reduced herbivory (H_R)		Ambient herbivory (H_A)	
	A_N $N = 37$	A_D $N = 31$	A_N $N = 34$	A_D $N = 32$
A. Effects of insect damage				
i. Per non-apical head	$N = 138$	$N = 146$	$N = 124$	$N = 96$
Flower head damage (%)	48.1 ± 2.6	48.4 ± 2.9	78.5 ± 2.5	72.9 ± 4.3
Potential seeds	141.1 ± 4.8	156.1 ± 4.4	157.0 ± 3.9	151.1 ± 4.6
Seeds matured	69.6 ± 7.5	99.0 ± 6.8	30.7 ± 5.3	31.5 ± 6.5
ii. Whole plant				
Total potential seeds	562.7 ± 55.1	721.8 ± 99.4	604.6 ± 64.6	446.4 ± 46.2
Undamaged seeds matured	355.9 ± 49.0	477.8 ± 81.8	186.3 ± 29.6	112.0 ± 27.9
B. Plant structural investment				
Plant height (cm)	53.3 ± 2.0	53.9 ± 2.1	50.6 ± 1.7	47.5 ± 1.9
Rosette diameter (cm)	32.2 ± 1.6	34.6 ± 1.7	34.0 ± 1.6	30.6 ± 1.4
Branches per plant (N)	5.2 ± 0.9	6.6 ± 0.6	5.9 ± 1.0	5.4 ± 0.4
Heads initiated per plant (N)	9.6 ± 0.9	12.6 ± 1.4	10.4 ± 1.8	10.2 ± 0.8
C. Plant-reproductive investment (excluding apical head)				
No. mature flower heads	2.9 ± 0.4	4.2 ± 0.6	2.8 ± 0.4	2.3 ± 0.3
Mature heads with seed (N)	1.9 ± 0.3	3.5 ± 0.5	1.5 ± 0.2	1.3 ± 0.2

the reduced herbivory treatment (Fig. 1a vs. Figure 1b). Although the insecticide treatment reduced flower head damage, there was no evidence that apical damage altered the intensity of cumulative floral herbivory on the later, lower flowering heads.

Initial plant size did not vary among treatments (MANOVA: $p_A = 0.59$, $F = 0.64$; $p_H = 0.67$, $F = 0.52$; Appendix 2 and 3Bi). Rosette diameters ranged 28–31 cm and apical floral bud diameters ranged 21–24 cm. At the start of data collection each year, plants averaged 3–4 flower head buds. No interaction occurred between apical damage treatment and subsequent herbivory treatment (MANOVA: $p_{A \times H} = 0.24$, $F = 1.42$). Thus, because initial conditions among treatments were comparable, final plant differences represent treatment responses.

Plant structural and reproductive investment

Neither apical damage treatment nor insect herbivory treatment had a significant effect on plant structural investment over the growing season (height, diameter, branches, flower buds: Table 1B) (MANOVA: $p_A = 0.22$, $F = 1.45$; $p_H = 0.18$, $F = 0.61$; $p_{A \times H} = 0.32$, $F = 1.19$; Appendix 3Bii). However, we found an interaction between treatments for plant-reproductive effort (Table 1C; $p_{A \times H} = 0.04$, $F = 3.32$; Appendix 3Biii). Apical damage did affect reproductive investment when herbivory was reduced ($p_{H \times R} = 0.02$; $F = 4.22$; Appendix 3Biv), but not under ambient herbivory ($p_{H \times A} = 0.37$; $F = 1.01$; Appendix 3Bv). The consequences of apical damage varied between herbivory treatments for both the number of heads that matured (= flowered; Table 1C; $p_{A \times H} = 0.03$,

$F = 5.10$; Appendix 3Ci) and that succeeded in producing undamaged viable seed (Table 1C; $p_{A \times H} = 0.01$, $F = 6.64$; Appendix 3Cii). The components of this outcome are as follows.

First, when cumulative herbivory over the season was reduced, the numbers of heads that matured were marginally higher ($p_{H \times R} = 0.05$, $F = 4.00$; Appendix 3Di), and the numbers that succeeded in producing undamaged viable seed ($p_{H \times R} = 0.007$, $F = 7.79$; Appendix 3Dii) were significantly higher on plants with apical damage than those without apical damage. These results provide evidence of a compensatory response to apical damage.

Second, apical damage made no difference in the total number of flower heads matured ($p_{H \times A} = 0.23$, $F = 1.48$; Appendix 3Ci) or in the number of mature, seed-producing heads under ambient cumulative herbivory ($p_{H \times A} = 0.70$, $F = 0.15$, Appendix 3Cii).

In sum, apical damage did not influence most of the parameters of plant structural investment within either herbivory treatment (Table 2: Q 1). However, when the cumulative herbivory was reduced, the total number of flower heads matured and producing seed increased in the apical damage treatment compared to the no apical damage treatment (Table 1). Thus, reduction in cumulative herbivory over the flowering season allowed us to quantify the magnitude of the effect of apical dominance release in response to damage and the resulting increase in seed-reproductive success. This compensatory response to apical damage was obscured for plants under the relatively high ambient level of floral herbivory observed.

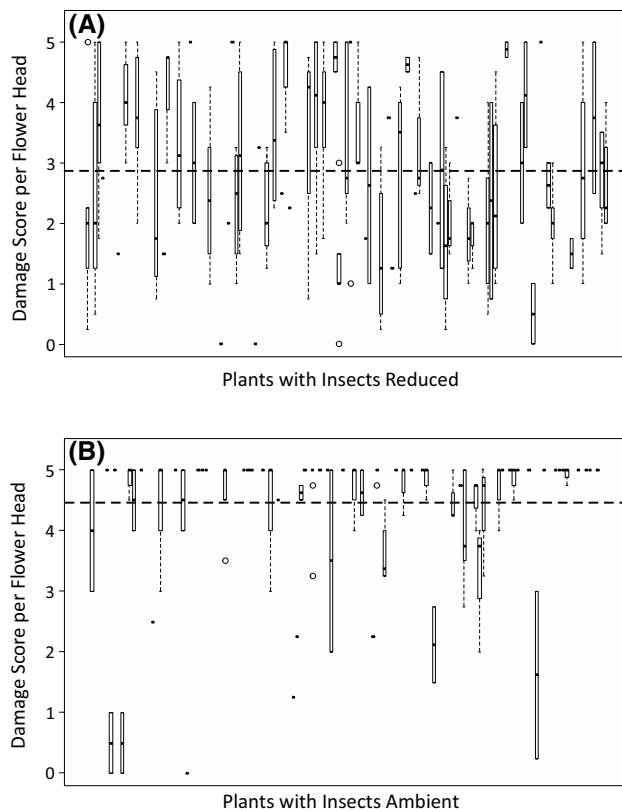


Fig. 1 Average insect damage score per lower, later (non-apical) flower head matured for each *C. canescens* plant (bold dashed line, distribution range is 95% CI) by herbivory treatment: **a** experimentally reduced herbivory ($N = 68$), and **b** ambient herbivory ($N = 66$). Plants are presented in a random order within treatment. Damage scores were based on the proportion of receptacle base, florets and developing seeds damaged by insects per head and averaged for all later (non-apical) flower heads per plant (1 = low to 5 = high)

Total seed production per plant

Early apical damage and cumulative floral herbivory over the season interactively influenced the number of undamaged seeds produced by a plant ($p_{A \times H} = 0.04$, $z = 2.03$, Table 1A; Appendix 4A). Plants were able to compensate for the apical head seed loss on average, as apical damage alone did not lead to a difference in average plant seed production ($p_{H:R} = 0.20$, $z = -0.27$; $p_{H:A} = 0.07$, $z = 1.79$; Table 1A; Appendix 4A). Although average seed production did not differ significantly between apical damage treatments, seed production increased 30% when apical damage was imposed under experimentally reduced floral herbivory, but decreased approximately 60% with apical damage under ambient floral herbivory. Consequently, herbivory reduction nearly doubled seed production in plants without apical damage (91%), and nearly quadrupled seed production with apical damage (391%) relative to plants under ambient herbivory (Table 1A).

Table 2 Qualitative summary of results

Treatment	Variables measured		
Q1: Apical damage response (reproductive investment)			
	Investment	# Heads	# Matured
Herbivory	*	*	*
Apical damage	*	n.s.	*
H × A	*	*	*
A: Reduced	*	*	*
A: Ambient	n.s.	n.s.	n.s.
<i>*Appendix</i>	<i>3Biii</i>	<i>3C.2i</i>	<i>3C.2ii</i>
Q2: Effects on plant fitness (seeds per plant)			
	# Undamaged	# Potential	% Realized
Herbivory	*	*	*
Apical damage	n.s.	n.s.	n.s.
H × A	*	*	*
A: Reduced	n.s.	n.s.	*
A: Ambient	n.s.	n.s.	*
<i>*Appendix</i>	<i>4A</i>	<i>4B.1</i>	<i>4B.2</i>
Q3: Effects on per-head contributions (seeds per flower head)			
	# Undamaged	# Potential	% Realized
Herbivory	*	n.s.	*
Apical damage	n.s.	n.s.	n.s.
Position	*	*	*
H × A	*	*	*
A × position	*	*	*
A: Reduced	n.s.	—	n.s.
Position	*	—	*
A × position	*	—	*
A: Ambient	n.s.	—	n.s.
Position	*	—	*
A × position	n.s.	—	n.s.
<i>*Appendix</i>	<i>4C</i>	<i>4D</i>	<i>4E</i>

Asterisks (*) indicate significant treatment or interaction effects, “n.s.” represents non-significant effects, and dashes (—) are indications of sub-analyses that were not performed. Full statistical tables for these analyses are provided in Appendices 3 and 4, and specific results references are indicated in italics within the table

The clearest effect of cumulative herbivory on the compensation response is represented in the difference in realized potential seed production with apical damage. Potential plant seed production, estimated from plant flower head sizes, had a similar pattern to observed plant seed production ($p_{A \times H} = 0.02$, $t = 2.41$, Table 1A; Appendix 4B). Seed production potential was only marginally reduced with apical damage under ambient herbivory ($p_{H:A} = 0.05$, $t = 2.0$), and the increase in fitness potential under reduced herbivory was not significantly different between apical damage treatments ($p_{H:R} = 0.15$, $t = -1.46$). However, degree to which actual, observed seed production realized the estimated plant seed production potential was significantly lower under ambient ($p_{A \times H} = 0.02$, $t = 2.41$; $p_{H:A} = 0.03$, $t = 2.25$, Fig. 2b;

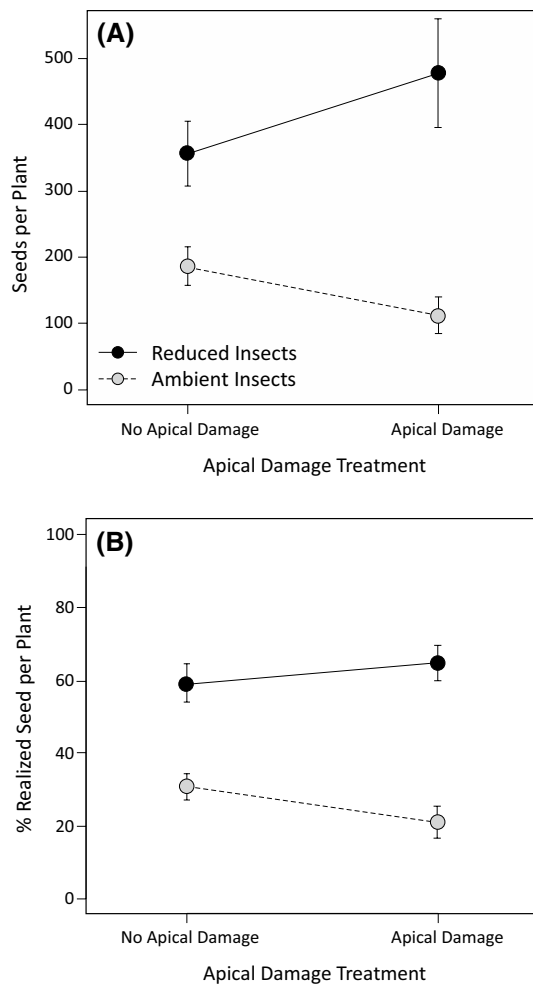


Fig. 2 Whole plant seed production for *C. canescens* (mean, SE: $N = 37$ and 31 (H_R : A_N and A_D); 34 and 32 (H_A : A_N and A_D)): **a** number undamaged viable seeds matured per plant and **b** percent of potential seed production that was realized per plant in each herbivory treatment by the later flower heads (excluding the apical head): insecticide-reduced herbivory (black, solid line) and ambient herbivory (gray, dashed line). Percent seed set realized is the count of undamaged matured seed in the field data divided by the estimate of potential seed production based on flower head sizes. Potential seed production by flower head size was estimated using the regression in Louda and Potvin (1995), and summed for all the flower heads recorded for each plant

Appendix 4C), but not different under reduced herbivory ($p_{H:R} = 0.27$, $t = -1.11$). Any potential for additional seed production with apical damage that might have increased fitness was eliminated under ambient herbivory (Table 2: Q2).

Within-plant distribution of seed production

Both apical head damage and herbivory treatments influenced overall fitness contributions from non-apical flowering heads. Apical damage, interacting with flower head position, led to more seed contribution from a greater

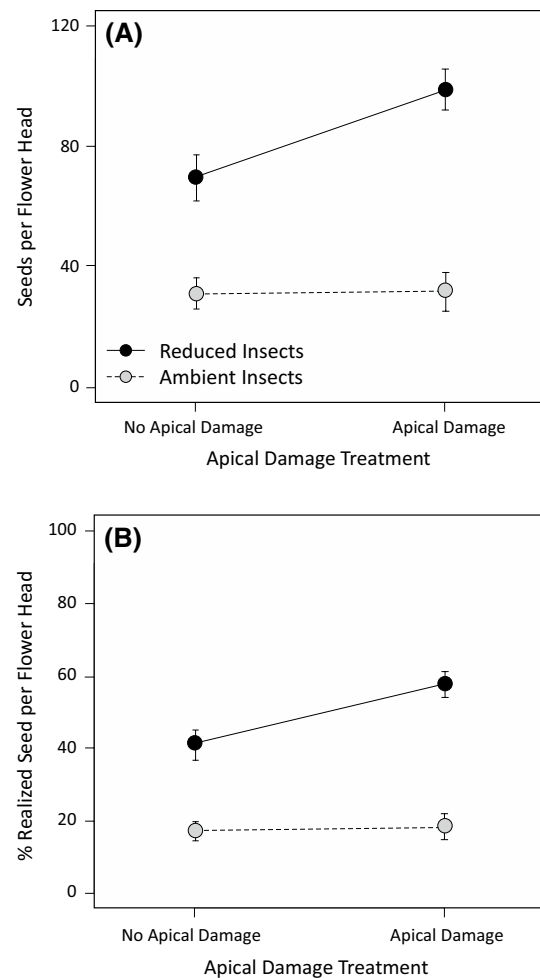


Fig. 3 Per flower head **a** number of undamaged viable seeds matured by *C. canescens* [mean, SE: $N_{heads} = 138$ and 146 (H_R : A_N and A_D); 124 and 96 (H_A : A_N and A_D)] and **b** percent of estimated potential seed that was realized, per flower head, by treatment. Percent of total initiated (potential) seed set actually realized is the actual matured seed counts from field data divided by potential seed production based on flower head sizes (regression in Louda and Potvin 1995)

range of lower positioned flower heads compared to undamaged plants ($p_{A \times position} = 0.01$, $t = -2.55$, Figs. 3a, 4, Appendix 4D). This result can be attributed to an increase in both potential ($p_{A \times position} = 0.04$, $t = -2.06$, Table 1, Appendix 4E) and estimated seed potential realized (proportion realized: $p_{A \times position} < 0.01$, $t = -2.66$; Fig. 3b; Table 1, Appendix 4Fi) per non-apical flower head. Herbivory reduction had significant main effects on both per-head seed production ($p_H < 0.01$, $t = -2.80$; Fig. 3d) and proportion of estimated seed production realized ($p_H < 0.01$, $t = -2.75$; Fig. 3b), but did not affect estimated potential seed production per flower head ($p_H = 0.95$, $t = -0.07$; Table 1; Appendix 4D).

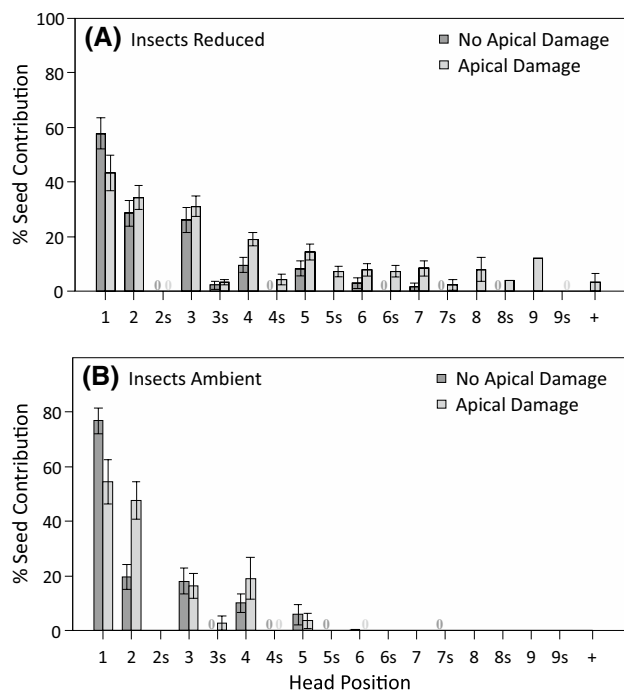


Fig. 4 Undamaged, mature seed contributed to total seed production for *C. canescens* by flower head position. Average percent of whole plant seed production contributed by each flower head position: **a** with experimentally reduced herbivory, versus **b** with ambient herbivory to subsequent heads. Values are mean (\pm SE) per plant percent total undamaged seeds per flower head by position for the apical treatments: no apical damage (black bars) and experimental apical damage (gray bars). The “s” heads are subsidiary heads below the branch terminal flower head; “+” refers to head/branch positions below the 9th branch (numbered 10–13 in this study); and, “0” indicates positions where heads flowered, but did not produce any undamaged, viable, seeds. $N_{\text{plants}} = 37$ and 31 (H_R : A_N and A_D); 34 and 32 (H_A : A_N and A_D)

Within herbivory treatments, this pattern was more nuanced. When herbivory was reduced, the interaction of apical damage and flower head position influenced per-head seed contributions (H_R : $p_{A \times \text{position}} = 0.03$, $t = -2.21$) and realized seed potential (H_R : $p_{A \times \text{position}} = 0.02$, $t = -2.32$; Fig. 4a). However, position alone related to both measures of seed contribution under ambient herbivory (undamaged seed H_A : $p_{\text{position}} = 0.01$, $t = -2.59$; proportion realized potential H_A : $p_{\text{position}} < 0.01$, $t = -3.40$) with no effect of apical damage (undamaged seed H_A : $p_A = 0.31$, $t = 1.01$; proportion realized potential H_A : $p_A = 0.51$, $t = 0.67$).

Therefore, the level of floral herbivory on subsequent, later flowering heads determined the actual, realized effect of apical damage on the within-plant distribution of undamaged seed produced (Table 2: Q3). Under reduced levels of cumulative herbivory over the season, plants in the early apical damage treatment produced a similar or slightly greater number of undamaged seeds than did plants in the no apical damage treatment. Compensation for early apical damage occurred, seen

as an increase in plant seed production related to an increase in the contribution of seed by later, lower flower heads to total plant seed production (Table 1, Fig. 4b), but only under the condition of reduced cumulative herbivory.

Discussion

Plant tolerance often occurs via a combination of traits, each of which contributes to compensation and helps minimize impacts on plant fitness (Wise et al. 2008). Flowering patterns resulting from strong apical control can provide a significant early season investment plus a reservoir of delayed flower heads to provide additional fitness through time. In *C. canescens*, both the disproportionate early season apical investment and seed production from additional flowers that arose after apical damage contributed to potential plant tolerance. However, this combination did not in general provide the average plant with a means of performing as well as an individual plant that experiences lower herbivory. Under ambient herbivory, the later developing, lower positioned flower heads were less likely to realize seed set, undercompensating for seed losses associated with early apical damage. Late season losses negated potential fitness gains from greater numbers of flower heads, and increased the value of apical seed production to whole plant fitness. Plant tolerance (the capacity to achieve fitness similar to undamaged plants) was sufficient to maintain fitness after apical damage, but could not compensate for the ambient cumulative herbivory losses accrued over the growing season.

Effect of apical damage on the distribution of within-plant flowering effort and success

Early apical damage did release apical dominance: apical damage increased the relative contribution of later, lower-positioned flower heads to total plant-realized seed production under reduced herbivory. This finding is consistent with other systems, where meristem release by apical damage provides a mechanism to compensate for fitness losses to herbivory in the field (e.g., Huhta et al. 2000; Juenger and Bergelson 2000; Klimešová et al. 2014).

Bet-hedging theory predicts that plants should keep reproductive resources in reserve to enable continued compensation in an uncertain herbivory environment (Nilsson et al. 1996; Childs et al. 2010). The effect of floral herbivory on *C. canescens* seed production is influenced by the synchrony of its floral herbivores with plant-flowering phenology (Russell and Louda 2005). Distributing reproductive effort over longer time periods may increase the probability that a subset of flower heads avoid damage. Later season flowers may have a higher probability of escaping specialist herbivores (e.g., *Erigeron glaucus*, English-Loeb and

Karban 1992). Flexible allocation to later-developing flowers (e.g., *Sanicula arctopoides*, Lowenberg 1994) or extended flowering time (e.g., *Helianthus annuus*, Pilsen and Decker 2002) can lead to greater compensation capacity. We hypothesize that continued investment in lower-positioned heads will allow some individuals to partition reproductive effort through time, increasing the flowering period, and providing a partial escape from herbivores. For instance, because the most common and one of the earliest native floral feeders on *C. canescens*, the tephritid fly *Paracantha culta*, oviposits preferentially on small flower heads (10–15 mm diameter, Lamp and McCarty 1982), investments across time may confer a “size escape” (i.e., Vail 1992) from adapted floral herbivores. With the large variation reported in both floral herbivory and plant seed production (Louda and Potvin 1995; Rose et al. 2005), these results demonstrate that the apical damage response could provide a tolerance mechanism through which *C. canescens* individuals might compensate in seed production under the risk of continuing, but variable, herbivory.

Interaction between apical damage and cumulative herbivory

Reproductive success and tolerance to herbivory, specifically in response to early-apical damage, was determined by interaction with the level of herbivory experienced. Although *C. canescens* plants had the potential to tolerate loss of the large, early apical flower head investment, such tolerance was insufficient on average to override the fitness costs imposed by cumulative floral herbivory. The relative advantage of high early investment, that escapes herbivores, compared to that of releasing additional investment to other flowers, likely varies extensively in time and space (i.e., Brody and Irwin 2012; Klimešová et al. 2014; Krimmel and Pearse 2016). For instance, Adhikari and Russell (2014) found a greater proportion of flowering heads developed in response to apical damage in another native thistle (*Cirsium altissimum*), but the fecundity of axillary flower heads was insufficient to provide compensatory seed production. Without apical damage, if ambient herbivory were low, it is a possible preferential apical investment and early-season inhibition of lower-positioned and axillary head development would still reduce seed contributions from later flowering heads. The typical apical contribution to total seed production by *C. canescens* (Fig. 4) is important. Undamaged apical heads produced 58–76% of total plant seed production on average. That sustained flower bud release after early apical damage enabled greater seed contributions from later heads with reduced herbivory suggests there may be a cost of apical dominance in lower herbivory environments (Aarssen 1995). A large investment in the apical head not only presumably mitigates the fitness costs of the high average

risk of cumulative floral herbivory but also the inhibition of later flower heads by apical dominance.

Effect of cumulative herbivory on success of response through apical damage

Under field conditions, individual *C. canescens* plants have the capacity to fully compensate, or possibly even over-compensate, for early loss of the apical flower head, if an individual escapes high-intensity ambient herbivory. Plants compensated fully for apical damage when cumulative herbivory was reduced on non-apical heads. Plants experiencing ambient floral herbivory were unable to increase their fitness relative to reduced herbivory conditions through the apical damage response (e.g., negative trend in seed production between apical damage treatments), and had comparatively lower fitness regardless of apical damage.

Effective compensation depends upon multiple interactions; response capacity, and the range of damage at which tolerance works, varies with ecological context. Plant resource condition, herbivore dynamics, phenological overlap with shared hosts and pollinators or competing predators, and timing of damage can influence the degree of plant tolerance (Kolb et al. 2007; Wise and Abrahamson 2007; von Euler et al. 2014; Lehndal and Ågren 2015; Krimmel and Pearse 2016; Stieha et al. 2016; Kafle et al. 2017). Co-occurring stressors may further interact with cumulative herbivory pressure to inhibit successful tolerance (Lay et al. 2011; Nguyen et al. 2016). Population-level effects of herbivory have been well-documented in *C. canescens*. We, therefore, evaluated the interaction between tolerance and the level of herbivory experienced. We detected under-compensation in response to the insect herbivore environment, rather than inherent constraints on plant ability to compensate.

The interaction between early apical damage and later intensity of herbivory suggests mechanisms that influence variation in herbivory risk and compensatory timing of *C. canescens* are likely to be particularly important. For example, experimental logistics meant we studied plants that were in relatively dense patches for this sparse native thistle (unpublished data). We hypothesize that if herbivory on *C. canescens* varies with plant density (i.e., Ehrlén 1996; Janovský et al. 2016; Underwood and Halpern 2012), then isolated individuals of *C. canescens* may encounter reduced herbivore loads, and be more likely to benefit from compensation in the field. Additionally, we did not compare differences in seed quality among treatments, though studies have shown compensatory responses may affect seed weight or germination probability rather than seed quantity (Pilsen and Decker 2002; Aikens and Roach 2015). Further studies are required to examine how environmental context influences fitness outcomes (i.e., Louda 1982; Gonzáles et al. 2008;

Banta et al. 2010), and determines the effectiveness of the tolerance mechanisms detected.

Conclusion

When monocarpic perennial plants are consistently exposed to intense floral herbivory, plant responses that increase tolerance for within-season reproductive losses to herbivores would be expected to provide an important contribution to plant fitness (Järemo and Palmqvist 2001; Aikens and Roach 2015). Both disproportionate apical investment and sustained bud release contributed to potential plant tolerance, increasing relative plant fitness when average cumulative herbivory was reduced. Based on observations, we hypothesize that such tolerance can benefit plants that escape the highest levels of insect herbivory, such as those that flower in lower density local environments. These results demonstrate the magnitude and tradeoffs of tolerance in response to variable floral herbivory and further our understanding of tolerance mechanisms that contribute to plant performance and population persistence under field conditions.

Author contribution statement NW and SL conceived and designed the experiments. NW performed the experiments and analyzed the data. NW and SL wrote the manuscript.

References

- Aarssen LW (1995) Hypotheses for the evolution of apical dominance in plants: implications for the interpretation of overcompensation. *Oikos* 74:49–156
- Adhikari S, Russell FL (2014) Effects of apical meristem mining on plant fitness, architecture, and flowering phenology in *Cirsium altissimum* (Asteraceae). *Am J Bot* 101:2079–2087
- Agrawal AA (2000) Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. *Trends Plant Sci* 5(7):309–313
- Agrawal AA (2005) Future directions in the study of induced plant responses to herbivory. *Entomol Exp Appl* 115:97–105
- Agrawal AA, Hastings AP, Johnson MTJ, Maron JL, Salminen J-P (2012) Insect herbivores drive real-time ecological and evolutionary change in plant populations. *Science* 338:113–116
- Aikens ML, Roach DA (2015) Potential impacts of tolerance to herbivory on population dynamics of a monocarpic herb. *Am J Bot* 102(11):1901–1911
- Banta JA, Stevens MHH, Pigliucci M (2010) A comprehensive test of the ‘limiting resources’ framework applied to plant tolerance to apical meristem damage. *Oikos* 119:359–369
- Brody AK, Irwin RE (2012) When resources don’t rescue: flowering phenology and species interactions affect compensation to herbivory in *Ipomopsis aggregata*. *Oikos* 121:1424–1434
- Brody AK, Price MV, Waser NM (2007) Life history consequences of vegetative damage in scarlet gilia, a monocarpic plant. *Oikos* 116(6):975–985
- Carmona D, Fornoni J (2013) Herbivores can select for mixed defensive strategies in plants. *New Phytol* 197:576–585
- Childs DZ, Metcalf CJE, Rees M (2010) Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. *Proc Royal Soc B* 277:3055–3064
- Ehrlén J (1996) Spatiotemporal variation in predispersal seed predation intensity. *Oecologia* 108:708–713
- English-Loeb GM, Karban R (1992) Consequences of variation in flowering phenology for seed head herbivory and reproductive success in *Erigeron glaucus* (Compositae). *Oecologia* 89:588–595
- Fornoni J (2011) Ecological and evolutionary implications of plant tolerance to herbivory. *Funct Ecol* 25:399–407
- González WL, Suárez LH, Molina-Montenegro MA, Gianoli E (2008) Water availability limits tolerance of apical damage in the Chilean tarweed *Madia sativa*. *Acta Oecologia* 34:104–110
- Gruntman M, Novoplansky A (2011) Ontogenetic contingency of tolerance mechanisms in response to apical damage. *Ann Bot* 108:965–973
- Huhta A, Lennartsson T, Tuomi J, Rautio P, Laine K (2000) Tolerance of *Gentianella campestris* in relation to damage intensity: an interplay between apical dominance and herbivory. *Evol Ecol* 14:373–392
- Janovský Z, Janovská M, Weiser M, Horčíčková E, Říhová D, Münzbergová Z (2016) Surrounding vegetation mediates frequency of plant–herbivore interactions in leaf-feeders but not in other herbivore groups. *Basic Appl Ecol* 17:352–359
- Järemo J, Palmqvist E (2001) Plant compensatory growth: a conquering strategy in plant–herbivore interactions? *Evol Ecol* 15:91–102
- Jongejans E, Shea K, Skarpaas O, Kelly D, Shepphard A, Woodburn T (2008) Dispersal and demography contributions to population spread of *Carduus nutans* in its native and invaded ranges. *J Ecol* 96:687–697
- Juenger T, Bergelson J (2000) The evolution of compensation to herbivory in scarlet gilia, *Ipomopsis aggregata*: herbivore-imposed natural selection and the quantitative genetics of tolerance. *Evolution* 54:764–777
- Kafle D, Hanel A, Lortzing T, Steppuhn A, Wurst S (2017) Sequential above- and belowground herbivory modifies plant responses depending on herbivore identity. *BMC Ecol* 17:5
- Kaul RB, Sutherland DM, Rolfsmeier SB (2007) The Flora of Nebraska. University of Nebraska-Lincoln, Lincoln
- Keeler KH, Harrison AT, Vescio LS (1980) The flora and Sandhills prairie community of Arapaho Prairie. *Prairie Nat* 12:65–78
- Klimešová J, Sosnová M, Martínková J (2007) Life-history variation in the short-lived herb *Rorippa palustris*: effect of germination date and injury timing. *Plant Ecol* 189:237–246
- Klimešová JM, Malíková L, Rosenthal J, Šmilauer P (2014) Potential bud bank responses to apical meristem damage and environmental variables: matching or complementing axillary meristems? *PLoS ONE* 9:e88093. <https://doi.org/10.1371/journal.pone.0088093>
- Kolb A, Leimu R, Ehrlén J (2007) Environmental context influences the outcome of a plant–seed predator interaction. *Oikos* 116:864–872
- Krimmel B, Pearse IS (2016) Tolerance and phenological avoidance of herbivory in tarweed species. *Ecology* 97(5):1357–1363
- Lamp WO (1980) Pre-dispersal seed predation of the Platte thistle and its effects on seed production. PhD Dissertation. University of Nebraska-Lincoln, Lincoln
- Lamp WO, McCarty MK (1981) Biology and ecology of the Platte thistle (*Cirsium canescens*). *Weed Sci* 29:686–692
- Lamp WO, McCarty MK (1982) Predispersal seed predation of a native thistle, *Cirsium canescens*. *Environ Ent* 11(4):847–851
- Lay CR, Linhart YB, Diggle PK (2011) The good, the bad and the flexible: plant interactions with pollinators and herbivores over space and time are moderated by plant compensatory responses. *Ann Bot* 108:749–763

- Lehndal L, Ågren J (2015) Latitudinal variation in resistance and tolerance to herbivory in the perennial herb *Lythrum salicaria* is related to intensity of herbivory and plant phenology. *J Evol Biol* 28:576–589
- Lehndal L, Hambäck PA, Ericson L, Ågren J (2016) Herbivory strongly influences among-population variation in reproductive output of *Lythrum salicaria* in its native range. *Oecologia* 180:1159–1171
- Lehtilä K (2000) Modelling compensatory regrowth with bud dormancy and gradual activation of buds. *Evol Ecol* 14:315–330
- Lennartsson T, Nilsson P, Tuomi J (1998) Induction of overcompensation in the field gentian *Gentianella campestris*. *Ecology* 79(3):1061–1072
- Louda SM (1982) Distribution ecology: variation in plant recruitment in relation to insect seed predation. *Ecol Monogr* 52:25–41
- Louda SM (1983) Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. *Ecology* 64:511–521
- Louda SM (1998) Population growth of *Rhinocyllus conicus* (Coleoptera: Curculionidae) on two species of native thistles in prairie. *Env Entomol* 27:834–841
- Louda SM, Potvin MA (1995) Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology* 76:229–245
- Louda SM, Potvin MA, Collinge SK (1990) Predispersal seed predation, postdispersal seed predation and competition in the recruitment of seedlings of a native thistle in Sandhills prairie. *Am Midl Nat* 124:105–113
- Louda SM, Kendall D, Connor J, Simberloff D (1997) Ecological effects of an insect introduced for the biological control of weeds. *Science* 277:1088–1090
- Low C, Ellner SP, Holden MH (2013) Optimal control and cold war dynamics between plant and herbivore. *Am Nat* 182(2):E25–E29
- Lowenberg GJ (1994) Effects of floral herbivory on maternal reproduction in *Sanicula arctopoides* (Apiaceae). *Ecology* 75(2):359–369
- Lucas-Barbosa D (2016) Integrating studies on plant–pollinator and plant–herbivore interactions. *Trends Plant Sci* 21(2):125–133
- McCall AC, Irwin RE (2006) Florivory: the intersection of pollination and herbivory. *Ecol Lett* 9:1351–1365
- Nguyen D, Rieu I, Mariani C, van Dam NM (2016) How plants handle multiple stresses: hormonal interactions underlying responses to abiotic stress and insect herbivory. *Plant Mol Biol* 91:727–740
- Nilsson P, Tuomi J, Åström M (1996) Bud dormancy as a bet-hedging strategy. *Am Nat* 147:269–281
- Paige KN (1992) Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. *Ecology* 73:2076–2085
- Pilson D, Decker KL (2002) Compensation for herbivory in wild sunflower: response to simulated damage by the head-clipping weevil. *Ecology* 83:3097–3107
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Rand TA, Louda SM (2012) Exotic weevil invasion increases floral herbivore community density, function, and impact on a native plant. *Oikos* 121:85–94
- Rose KE, Louda SM, Rees M (2005) Demographic and evolutionary impacts of native and invasive insect herbivores on *Cirsium canescens*. *Ecology* 86:453–465
- Russell FL, Louda SM (2005) Indirect interaction between two native thistles mediated by an invasive exotic floral herbivore. *Oecologia* 146:373–384
- Starrfelt J, Kokko H (2012) Bet-hedging—a triple trade-off between means, variances and correlations. *Biol Rev* 87:742–755
- Stieha CR, Abbott KC, Poveda K (2016) The effects of plant compensatory regrowth and induced resistance on herbivore population dynamics. *Am Nat* 187(2):167–181
- Stowe KA, Marquis RJ, Hochwender CG, Simms EL (2000) The evolutionary ecology of tolerance to consumer damage. *Ann Rev Ecol Syst* 31:565–595
- Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. *Trends in Ecol Evol* 14:179–185
- Tenhumberg B, Louda SM, Eckberg JO, Takahashi M (2008) Monte-Carlo analysis of parameter uncertainty in matrix models of the weed *Cirsium vulgare*. *J Appl Ecol* 45:438–447
- Underwood N, Halpern SL (2012) Insect herbivores, density dependence, and the performance of the perennial herb *Solanum carolinense*. *Ecology* 93(5):1026–1035
- Vail SP (1992) Selection for overcompensatory plant responses to herbivory: a mechanism for the evolution of plant–herbivore mutualism. *Am Nat* 139:1–8
- Von Euler T, Ågren J, Ehrlén J (2014) Environmental context influences both the intensity of seed predation and plant demographic sensitivity to attack. *Ecology* 95(2):295–504
- Wise MJ, Abrahamson WG (2007) Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. *Am Nat* 169:443–454
- Wise MJ, Cummins JJ, De Young C (2008) Compensation for floral herbivory in *Solanum carolinense*: identifying mechanisms of tolerance. *Evol Ecol* 22:19–37

Appendix 1. Variation in Apical Damage Treatment Effectiveness

The apical damage treatment varied in its effectiveness in simulating the severe damage observed in the field (Figure A-1.1A). We examined the effects of this variation since any damage that affects apical regions can result in release of the axillary buds (Cline 1991). Also, plants vary in the strength of their response to apical damage, and the sensitivity of buds to apical inhibition is an important aspect of tolerance capacity (Tuomi *et al.* 1994, Nilsson *et al.* 1996).

In the control treatment, with no experimental damage imposed and insecticide protection, we expected large numbers of filled, undamaged seeds in the apical head; however, we found that some apical flower heads were severely damaged anyway and, so, developed 0 or only a few seeds (< 100) (Figure A-1.1B). Alternately, in the experimental damage treatment, with insect and mechanical experimental damage imposed, we expected few filled seeds in the apical flower head; however, we found that some of the experimentally damaged apical flower heads succeeded in producing a large number of seeds (≥ 150 seeds). Consequently, our analysis compared treatment effects for plants that had low apical damage (< 100 undamaged seeds), as intended for the undamaged apical treatment, versus those that had high apical damage (≥ 150 seeds), as intended for the damaged apical treatment (Figure A-1.1B).

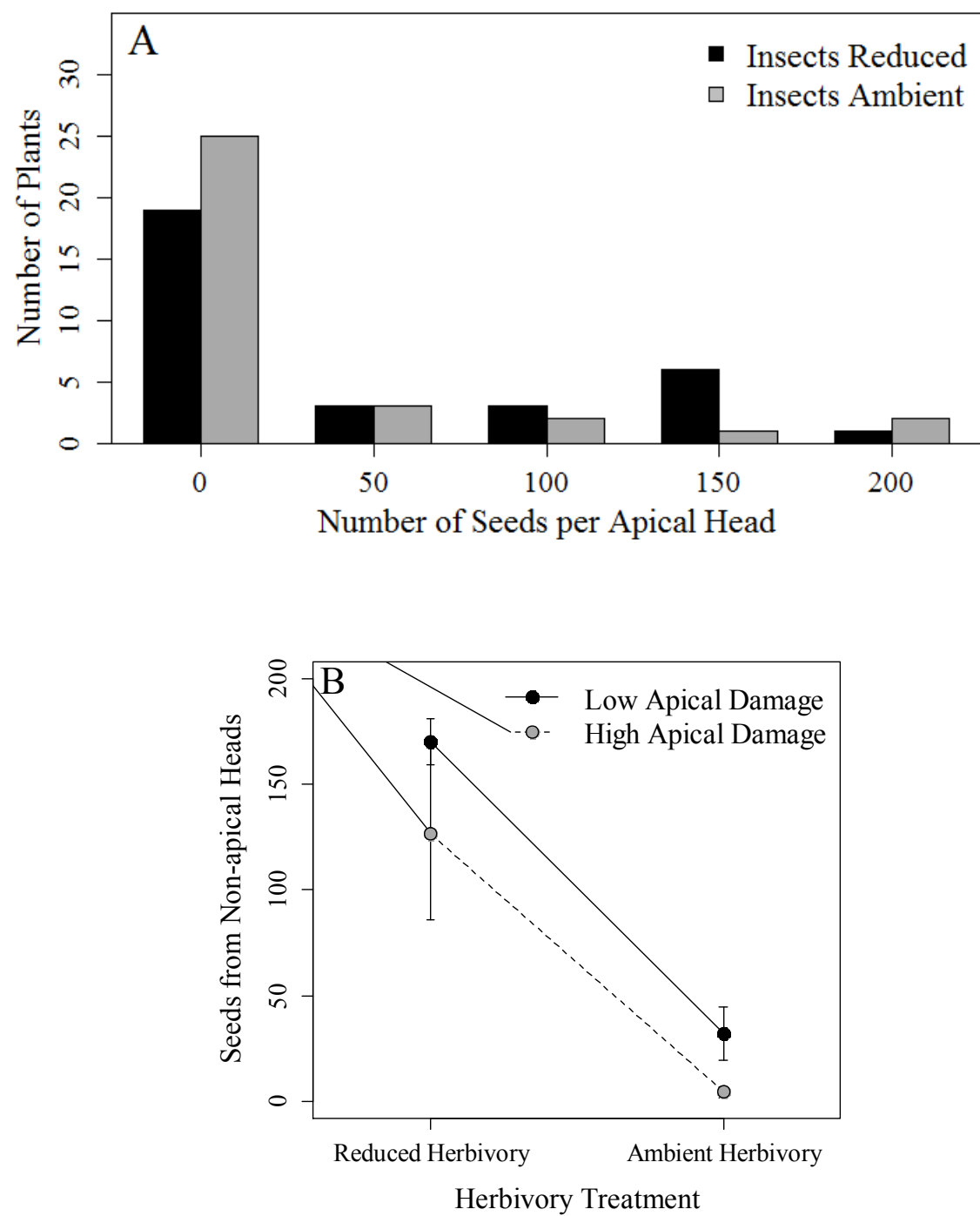
In this contrast, three key results emerged. First, plants with low damage to the apical flower head produced as many, but not more, seeds in later flower heads on average as plants with high apical damage, under reduced subsequent herbivory. Second, under ambient subsequent herbivory conditions, the plants with low damage to the apical head produced more undamaged seeds per later, lower flower head than did plants with high damage to the apical head. Third, when examined as the proportion of the potential number of seeds that were actually realized, the pattern of response to high versus low level of apical damage was similar per flower

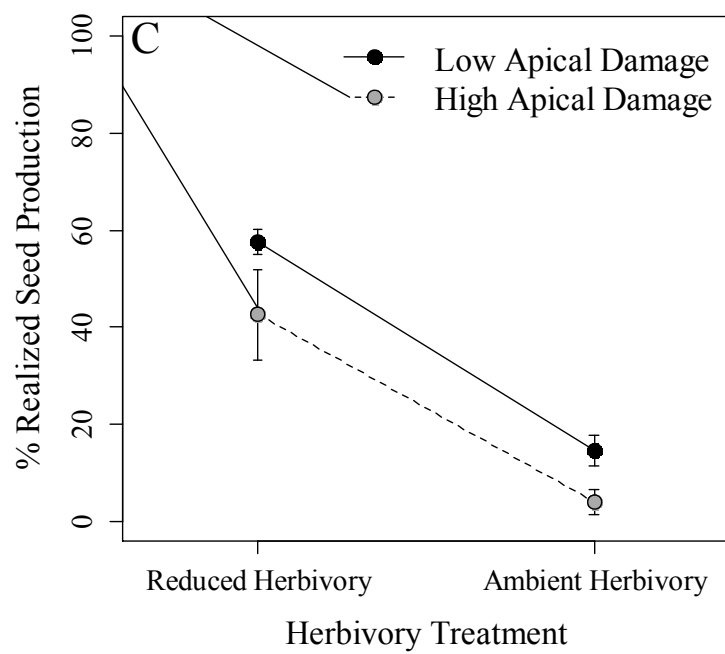
head, but stronger (Figure A-1.1C). The results provide evidence of compensatory ability for the early loss of the apical seeds but, contrary to initial expectation, the average contribution by later heads was greater on plants with low damage, rather than with high damage, to the apical flower head.

Figure Legends

FIG. A-1.1 Evaluating the consistency of apical damage treatment. (A) Frequency distribution of plants by number of undamaged seeds per apical flower head in the apical damage treatment for both subsequent herbivory treatments (experimentally reduced vs. ambient subsequent herbivory). The distributions demonstrate the variation in severity in the apical damage resulting from the treatment imposed (insect and mechanical damage: see Methods) and, so, the effectiveness of the imposed treatment. (B) Number of filled, undamaged seeds per non-apical flower head by treatment on plants with either low damage (> 150 undamaged seeds produced) or high damage (< 100 undamaged seeds produced) to the apical flower head as intended in the apical damage treatment ($n = 5$ per category); (C) Percent of realized potential seed production per later (non-apical) flower head on plants with either low damage or high damage to the apical flower head; expected potential seed production by flower head size estimated with regression in Louda & Potvin (1995).

Figure A-1.1





Appendix 2. Initial size by treatment

Initial size parameters for experimental *Cirsium canescens* plants by subsequent treatment; treatments manipulated both damage to the initial (apical) flower head (A_D = Apical damaged; A_N = Apical not damaged) and insect feeding (H_R = Herbivory reduced; H_A = Herbivory ambient) on subsequently produced flower heads during the season (2007, 2008) at Arapaho Prairie, NE. Values presented represent mean (\pm SE).

Variable	Year*	<u>Apical Head Damaged</u> <u>(A_D)</u>		<u>Apical Head Undamaged</u> <u>(A_N)</u>	
		H _R	H _A	H _R	H _A
Rosette Diameter					
	2007	37.3 (±2.6) ^a	32.7 (±1.3) ^a	33.2 (±2.0) ^a	37.5 (±2.0) ^a
	2008	26.9 (±1.6) ^b	25.3 (±1.4) ^b	29.6 (±2.2) ^b	27.2 (±1.7) ^b
	Overall	31.1 (±1.7)	28.4 (±1.1)	31.1 (±1.5)	31.9 (±1.6)
Apical Bud Diameter					
	2007	31.4 (±1.9) ^a	29.6 (±1.6) ^a	29.9 (±1.6) ^a	33.2 (±2.2) ^a
	2008	17.5 (±1.6) ^b	15.5 (±1.3) ^b	17.4 (±1.7) ^b	16.4 (±1.5) ^b
	Overall	23.2 (±1.7)	21.5 (±1.6)	22.8 (±1.6)	24.0 (±1.9)
Number of Buds					
	2007	5.4 (±1.0) ^a	4.5 (±0.4) ^a	3.9 (±0.5) ^a	5.6 (±0.9) ^a
	2008	3.0 (±0.5) ^b	2.3 (±0.3) ^b	2.8 (±0.5) ^b	2.9 (±0.5) ^b
	Overall	<u>4.0 (+0.5)</u>	<u>3.2 (+0.3)</u>	<u>3.2 (+0.4)</u>	<u>4.1 (+0.5)</u>
N	2007	13	14	15	15
	2008	32	33	35	33

Appendix 3. Details underlying statistical results

In the analyses of treatment effects on initial and end-of-season plant characters, bolded values indicate significant effects reported in the Results for: (A) Insect damage per flower head by treatment; with (B) MANOVA tables (with Pillai's trace test statistic) for initial and end-of-season plant characters. Dependent variables included in (i) are: average rosette diameter; apical bud diameter; and number of flower buds. Plant structure response variables included in (ii) are: plant height, average rosette diameter, number of flower buds, and number of branches. Plant reproductive response variables in (iii) are: number of flowered heads and number of heads with matured seeds. Finally, (C and D) present separate ANOVA tables and subsequent ANOVAs for each of the dependent variables included as measures of plant reproductive investment. Response variables are: (i) number of flowered heads, and (ii) number of heads with matured seeds.

(A) Treatment effects on insect damage per *C. canescens* flower head (Mixed Model GLM, plant as random effect)

Source	Value	Std. Error	DF	t-value	p-value
Intercept	0.468	0.0478	279	9.801	<0.001*
Apical Damage (<i>A</i>)	0.031	0.0664	127	0.464	0.644
Herbivory (<i>H</i>)	0.409	0.0699	127	5.857	<0.001*
<i>A</i> x <i>H</i>	-0.007	0.0966	127	-0.075	0.940

(B) Treatment effects on plant characters (MANOVA)

Source	Pillai's	Approx. F	num Df	dens DF	Pr(>F)
<i>(i.) Initial Measurements</i>					
Apical Damage (<i>A</i>)	0.015	0.637	3	125	0.593
Herbivory (<i>H</i>)	0.012	0.522	3	125	0.668
Year	0.546	50.209	3	125	<0.001*
<i>A</i> x <i>H</i>	0.032	1.415	3	125	0.242
<i>(ii.) Plant Structural Investment</i>					
Apical Damage (<i>A</i>)	0.044	1.449	4	126	0.222
Herbivory (<i>H</i>)	0.0488	1.615	4	126	0.175
Year	0.167	6.33	4	126	<0.001*
<i>A</i> x <i>H</i>	0.037	1.193	4	126	0.317
<i>(iii.) Plant Reproductive Investment</i>					
Apical Damage (<i>A</i>)	0.078	5.419	2	128	<0.001*
Herbivory (<i>H</i>)	0.1075	7.704	2	128	<0.001*
Year	0.104	7.394	2	128	<0.001*
<i>A</i> x <i>H</i>	0.049	3.324	2	128	0.039*
<i>(iv.) Reproductive Investment: Reduced Herbivory</i>					
Apical Damage (<i>A</i>)	0.12	4.22	2	64	0.019*
Year	0.17	6.64	2	64	0.002*
<i>(v.) Reproductive Investment: Ambient Herbivory</i>					
Apical Damage (<i>A</i>)	0.03	1.008	2	62	0.371
Year	0.19	7.18	2	62	0.002*

(C) Separate treatment effects on measures of reproductive investment (ANOVA)

Source	Sum Sq	Df	F value	Pr(>F)
<i>(i.) No. of Heads that Flowered</i>				
Apical Damage (<i>A</i>)	5.82	1	0.9813	0.324
Herbivory (<i>H</i>)	28.69	1	4.8413	0.030*
Year	11.95	1	2.0171	0.158
<i>A x H</i>	30.18	1	5.0937	0.026*
Residuals	764.44	129		
<i>(ii.) No. of Heads that Flowered with Seeds</i>				
Apical Damage (<i>A</i>)	18.62	1	4.9973	0.027*
Herbivory (<i>H</i>)	45.87	1	12.3131	<0.001*
Year	4.17	1	1.1207	0.292
<i>A x H</i>	24.73	1	6.6392	0.011*
Residuals	480.53	129		

(D) Separate components of reproductive investment within herbivory treatments

Source	Sum Sq	Df	F value	Pr(>F)
<i>(i.) Number of Heads Flowered</i>				
<i>Reduced Herbivory</i>				
Apical Damage (A)	32.79	1	4.0043	0.050*
Year	36.7	1	4.4817	0.038*
Residuals	532.29	65		
<i>Ambient Herbivory</i>				
Apical Damage (A)	4.829	1	1.4764	0.229
Year	1.364	1	0.4171	0.521
Residuals	206.046	63		
<i>(ii.) Number of Heads Flowered with Seeds</i>				
<i>Reduced Herbivory</i>				
Apical Damage (A)	44.35	1	7.7925	0.007*
Year	0.8	1	0.1402	0.709
Residuals	369.91	65		
<i>Ambient Herbivory</i>				
Apical Damage (A)	0.244	1	0.1539	0.696
Year	14.305	1	9.0398	0.004*
Residuals	99.695	63		

Appendix 4. Analyses of treatment effects on potential and realized seed production

Bolded values indicate significant effects reported in the Results; (A) Total seed production per plant; (B) MANOVA tables (1 – 3) for analyses of per plant potential and realized seed production (1) and Separate ANOVA tables for per plant potential (2) and realized seed production(3); (C) MANOVA table for per flower head per plant analysis of potential and realized seed production; (D) Separate ANOVA tables for per flower head per plant potential seed production and for realized seed production; and, (E) Results of the analysis of seed production by head position on a plant.

(A) Total seed production per plant (GLM, negative binomial distribution)

Source	Estimate	Std. Error	z-value	P(> z)	Null df	Residual df
<i>Good Seeds per Plant</i>						
Intercept	6.4205	0.2481	25.882	<0.001*	133	129
Apical Damage (<i>A</i>)	-0.2893	0.2927	-0.989	0.320		
Herbivory (<i>H</i>)	-1.5756	0.3032	-5.197	<0.001*		
Year (2008)	-0.3756	0.2109	-1.781	0.075		
<i>A x H</i>	0.8435	0.4166	2.025	0.043*		
<i>Reduced Herbivory</i>						
Intercept	6.1691	0.220	27.612	<0.001*	67	66
Apical Damage (<i>A</i>)	-0.296	0.233	-1.270	0.204		
Year	0.135	0.238	0.566	0.571		
<i>Ambient Herbivory</i>						
Intercept	5.054	0.315	16.054	<0.001*	65	64
Apical Damage (<i>A</i>)	0.615	0.345	1.786	0.074		
Year	-0.856	0.347	-2.468	0.014*		

(B) Total potential seeds per plant

Source	Estimate	Std. Error	t-value	P(> t)	Null df	Residual df
<i>(i.) Potential Seeds per Plant</i>						
Intercept	741.18	81.56	9.087	<0.001	136	132
Apical Damage (<i>A</i>)	-158.68	95.65	-1.659	0.010		
Herbivory (<i>H</i>)	-275.96	98.92	-2.79	0.006*		
Year (2008)	-32.65	69.15	-0.472	0.638		
<i>A x H</i>	316.31	136.54	2.317	0.022*		
<i>(ii.) Reduced Herbivory</i>						
Intercept	721.8	80.42	8.975	<0.001	69	68
Apical Damage (<i>A</i>)	-159.06	109.15	-1.457	0.150		
<i>(iii.) Ambient Herbivory</i>						
Intercept	446.43	56.89	7.848	<0.001	66	65
Apical Damage (<i>A</i>)	158.18	79.86	1.981	0.052		

(C) Total realized seed production

Source	Estimate	Std. Error	t-value	P(> t)	DF
<i>(i.) Percent Realized Seed Potential per Plant</i>					
Intercept	0.775	0.048	16.044	<0.001	132
Apical Damage (<i>A</i>)	-0.063	0.060	-1.050	0.296	
Herbivory (<i>H</i>)	-0.417	0.062	-6.677	<0.001	
<i>A x H</i>	0.208	0.086	2.411	0.017	
<i>(ii.) Reduced Herbivory</i>					
Intercept	0.773	0.042	18.294	0	67
Apical Damage (<i>A</i>)	-0.064	0.057	-1.110	0.271	
<i>(iii.) Ambient Herbivory</i>					
Intercept	0.363	0.066	5.484	0	64
Apical Damage (<i>A</i>)	0.143	0.064	2.248	0.028	

(D) Mature seeds produced per flower head by head position (Mixed Model GLM, plant as random effect)

Source	Value	Std.Error	DF	t-value	p-value
<i>(i.) Good Seeds by Head Position</i>					
Intercept	134.388	14.118	274	9.519	<0.001
Apical Damage (<i>A</i>)	3.520	21.204	127	0.166	0.868
Herbivory (<i>H</i>)	-74.133	26.463	127	-2.801	0.006
Head Position (<i>Pos</i>)	-0.102	0.029	274	-3.464	0.0006
<i>A</i> x <i>H</i>	17.117	35.343	127	0.484	0.629
<i>A</i> x <i>Pos</i>	-0.129	0.050	274	-2.554	0.011
<i>H</i> x <i>Pos</i>	-0.008	0.074	274	-0.106	0.916
<i>A</i> x <i>H</i> x <i>Pos</i>	0.072	0.097	274	0.745	0.457
<i>(ii.) Reduced Herbivory</i>					
Intercept	133.309	16.083	172	8.289	<0.001
Apical Damage (<i>A</i>)	4.036	24.211	64	0.167	0.868
Head Position (<i>Pos</i>)	-0.100	0.034	172	-2.953	0.004
<i>A</i> x <i>Pos</i>	-0.128	0.058	172	-2.207	0.029
<i>(iii.) Ambient Herbivory</i>					
Intercept	63.269	16.344	103	3.871	0.0002
Apical Damage (<i>A</i>)	21.033	20.739	63	1.014	0.314
Head Position (<i>Pos</i>)	-0.126	0.049	103	-2.589	0.011
<i>A</i> x <i>Pos</i>	-0.058	0.059	103	-0.981	0.329

(E) Estimated seed production per flower head (Mixed Model GLM, plant as random effect)

Source	Value	Std.Error	DF	t-value	p-value
<i>Estimated Potential Seeds by Head Position</i>					
Intercept	183.8833	9.461253	274	19.4354	0
Apical Damage (<i>A</i>)	3.22079	14.20232	127	0.226779	0.821
Herbivory (<i>H</i>)	-1.19875	17.71206	127	-0.06768	0.946
Head Position (<i>Pos</i>)	-0.07501	0.019652	274	-3.81683	<0.001*
<i>A</i> x <i>H</i>	-10.4521	23.65633	127	-0.44183	0.659
<i>A</i> x <i>Pos</i>	-0.06946	0.033732	274	-2.05922	0.040*
<i>H</i> x <i>Pos</i>	-0.04333	0.049557	274	-0.87433	0.383
<i>A</i> x <i>H</i> x <i>Pos</i>	0.11616	0.064562	274	1.799157	0.073

(F) Realized seed production per flower head (Mixed Model GLM, plant as random effect)

Source	Value	Std.Error	DF	t-value	p-value
<i>(i.) Percent Realized Seed by Head Position</i>					
Intercept	0.874947	0.073764	274	11.86139	0
Apical Damage (<i>A</i>)	-0.01512	0.110129	127	-0.13731	0.891
Herbivory (<i>H</i>)	-0.37526	0.136411	127	-2.75094	0.007*
Head Position (<i>Pos</i>)	-0.00056	0.000149	274	-3.76582	<0.001*
<i>A</i> x <i>H</i>	0.095597	0.182247	127	0.524546	0.601
<i>A</i> x <i>Pos</i>	-0.00068	0.000256	274	-2.65776	0.008*
<i>H</i> x <i>Pos</i>	-0.00027	0.000377	274	-0.72299	0.470
<i>A</i> x <i>H</i> x <i>Pos</i>	0.000457	0.00049	274	0.932217	0.352
<i>(ii.) Reduced Herbivory</i>					
Intercept	0.87312	0.079597	171	10.96925	0
Apical Damage (<i>A</i>)	-0.01858	0.119426	64	-0.1556	0.877
Head Position (<i>Pos</i>)	-0.00055	0.000165	171	-3.35596	0.001*
<i>A</i> x <i>Pos</i>	-0.00066	0.000283	171	-2.31703	0.022*
<i>(iii.) Ambient Herbivory</i>					
Intercept	0.518232	0.094236	103	5.499275	0
Apical Damage (<i>A</i>)	0.079903	0.120107	63	0.665266	0.508
Head Position (<i>Pos</i>)	-0.00093	0.000274	103	-3.40359	<0.001*
<i>A</i> x <i>Pos</i>	-0.00022	0.00033	103	-0.6569	0.513